Amer. Malac. Bull. **27**: 59-68 (2009)

Land snail models in island biogeography: A tale of two snails*

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Abstract: Oceanic islands have long been important in evolutionary biology. Land snails are a major component of oceanic island biotas and have much to offer as systems for addressing major questions in evolution and biogeography. We review patterns of within-archipelago biogeography and diversification in two large Hawaiian land snail groups, the Succineidae and the Achatinellinae. Molecular studies suggest that long-distance oceanic dispersal and colonization of the Hawaiian Islands has been rare but between-island dispersal has been far more common. Long-distance oceanic dispersal is the most important driver for deep phylogenetic divergence. Dispersal is also important within the archipelago, while among-island vicariant processes result in only a portion of tip clade diversity. The Achatinellinae are monophyletic but there is evidence of a deep phylogenetic split between the two Hawaiian succineid clades, a result of two independent colonizations reflecting two oceanic dispersal events. Hawaiian succineids have also dispersed to Samoa and Tahiti. Dispersal is an important biogeographical phenomenon, and its role in shaping distributions of island lineages should not be underestimated. Because of their relatively sedentary nature, yet a proclivity for long-distance passive dispersal, island snails can facilitate insights into mechanisms of evolutionary diversification. Important phylogenetic lessons are emerging from studies of island snails and such studies will eventually allow estimation of ages of species groups, speciation rates, timing of the processes involved in community assembly, and other dynamics, all of which are important contributions to the overall understanding of evolution.

Key words: Succineidae, Achatinellinae, phylogeography, vicariance, Hawaii

Islands have long been considered important model systems for the study of evolution and biogeography. In the Pacific, the Hawaiian and Galapagos Islands in particular have provided numerous novel scientific insights (*e.g.*, Cain 1984, Grant 1986). Land snails are an important component of biodiversity in many oceanic island groups (*e.g.*, Cowie 2004, Cameron *et al.* 2007) and have great potential as informative models with which to address major evolutionary, especially biogeographic, questions.

Specific biological attributes of island snails that render them informative as models for biogeographic analyses include their high levels of species endemism and often broad distributions of families. This allows phylogenetic studies to use a hierarchical systematic approach to illuminate nested evolutionary patterns from the levels of populations to families. A number of snail families have remarkable passive dispersal and colonization abilities, given geological time, in seeming contrast with their low active mobility and often relatively small spatial ranges at the species level (*e.g.*, Barker and Mayhill 1999, Fontaine *et al.* 2007). Certain land snails are adept at dispersing across vast geographic distances, including ocean basins. This has been widely acknowledged and documented (*e.g.*, Darwin 1859, Anonymous 1936, Rees 1965, Dundee *et al.* 1967, Vagvolgyi 1975) and is evidenced by the worldwide distributions of a number of lineages. It is now supported by molecular evidence (Gittenberger *et al.* 2006).

In this paper, we review the phylogenetics, biogeography, and phylogeography of two major groups of land snails, the Succineidae and Achatinellinae, that have diversified across the Hawaiian archipelago in contrasting ways, illustrating the value of studies of island snails in evolution and biogeography. Within each group, we first address interspecific phylogenetic relationships and colonization patterns and then focus on intraspecific phylogeography. Since the Hawaiian land snail fauna is highly threatened (Solem 1990, Lydeard *et al.* 2004), understanding diversification patterns and evolutionary history can also provide valuable insights for conservation (*e.g.*, Holland and Hadfield 2002).

THE HAWAIIAN ISLANDS AND THEIR BIOTA

The Hawaiian archipelago consists of a sequence of oceanic islands formed as the Pacific plate moves northwestward over a stationary "hot spot" in the earth's mantle. The hot spot sends magma up through the plate, creating a chain

* From the symposium "Molluscs as models in evolutionary biology: from local speciation to global radiation" presented at the World Congress of Malacology, held from 15 to 20 July 2007 in Antwerp, Belgium.

of volcanoes, each sequentially younger than the one that preceded it, northwestward away from the hot spot. High islands eventually subside and erode to become low atolls, then submerged seamounts, and are ultimately subducted as the Pacific plate slides under the adjacent tectonic plate (Price and Clague 2002). The current islands are divided into the younger "high" islands and the older northwestern islands, which have become low atolls or small, eroded pinnacles or islets. Currently, the oldest, northwestern-most island is Kure Atoll (29 Ma) and the oldest high island is Kauai (5.1 Ma), with the youngest island, Hawaii itself, being less than 0.5 Ma and still forming.

The islands harbor unique forms of plants and animals that are the products of evolution in isolation over tens of millions of years, as older islands vanished and new islands formed. Most of the current diversity occurs on the high islands, from the island of Kauai in the northwest to the island of Hawaii in the southeast (Fig. 1). The islands' extreme isolation, diversity of microhabitats, and dynamic geology have led to spectacular biological endemism as well as prominence as a global biodiversity hotspot (Simon 1987, Ziegler 2002). The unique, terrestrial evolutionary radiations have attracted scientific attention for over a century (Gulick 1905, Carson 1987, Wagner and Funk 1995, Hormiga *et al.* 2003). In recent decades, however, the Hawaiian biota has become increasingly threatened. Anthropogenic habitat destruction and the devastating impacts of non-native species (Staples and Cowie 2001, Eldredge and Evenhuis 2003) have led to high levels of extinction (Vitousek 1988, Pimm *et al.* 1994, Wagner *et al.* 1999).

There are over 750 nomenclaturally valid, native, land snail species in 11 families in the Hawaiian Islands; over 99% of these species are endemic (Cowie 1995, Cowie *et al.* 1995). It has long been assumed that each endemic group (genus, subfamily, family) of species within this huge diversity has resulted from *in situ* speciation following a single colonization by a single ancestral lineage (Zimmerman 1948) although until recently this had not been rigorously tested. Ascertaining biogeographic origins of land snail radiations is important for understanding their natural history, and the fact that multiple origins have now been demonstrated in some Hawaiian terrestrial invertebrate groups (Gillespie *et al.* 1994, Robinson and Sattler 2001, Rundell *et al.* 2004) suggests that other taxa may have similarly complex evolutionary histories.

Hawaiian land snails have suffered higher levels of extinction than perhaps any other group of Hawaiian organisms, with estimates as high as 90% of species now extinct (Cowie 2001) and most of the remainder seriously threatened. As a consequence of their present conservation status, there is an urgent need for data regarding the systematics and evolutionary history of the fauna, especially as legislative decisions regarding conservation require an unambiguous understanding of taxonomic status (*e.g.*, Avise 2000, Holland and Hadfield 2004, 2007).

COMPARATIVE BIOGEOGRAPHY

Integration of molecular phylogenetics with geological history is a powerful approach that permits estimation of lineage ages and polarity. Knowing absolute island ages, questions regarding temporal aspects of radiations such as rates of evolutionary diversification can be addressed; DNA sequences can provide high resolution, quantitative data relevant, for instance, to colonization patterns of many taxa including endemic terrestrial snails (Chiba 1999, Goodacre 2002, Holland and Hadfield 2002, Rundell *et al.* 2004, Holland and Cowie 2007).

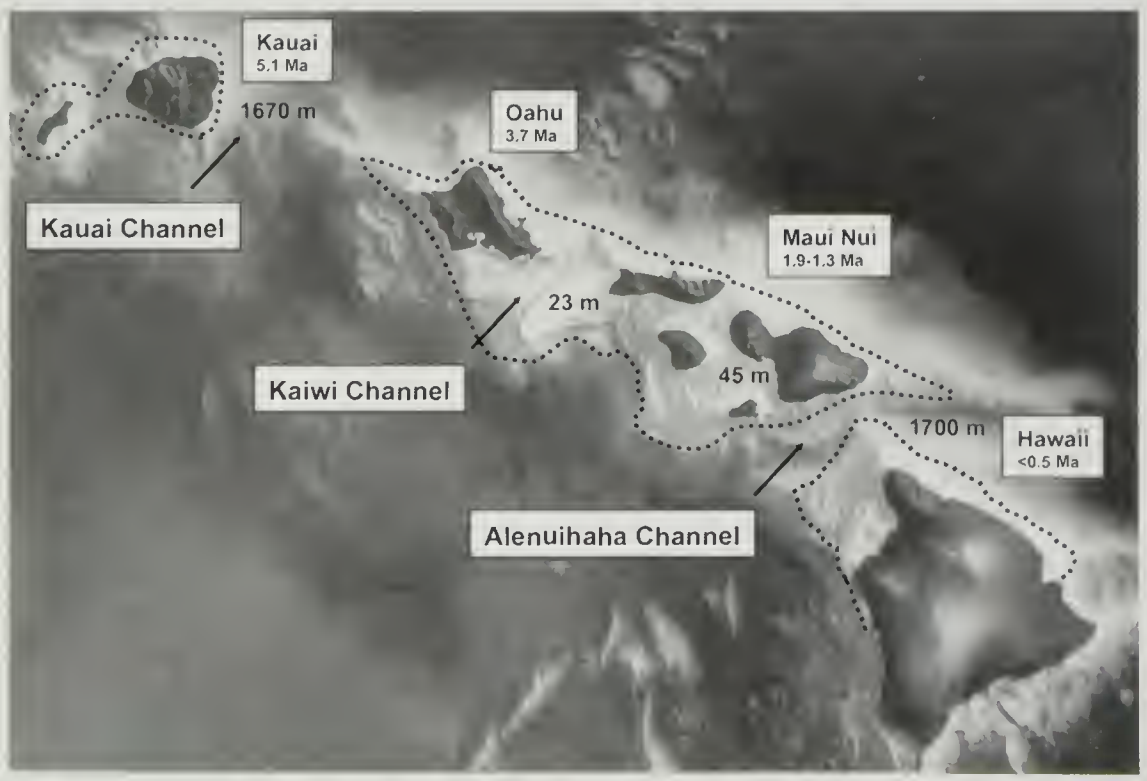

Figure 1. Map of the main Hawaiian Islands showing submarine topography and selected channel depths. Dotted lines show now submerged, maximum historical shorelines for each volcano as it formed. The islands of Maui, Lanai, Molokai, and Kahoolawe are known as Maui Nui. These islands and Oahu formed a single super island as recently as 18,000 years ago during the last glacial maximum.

Molecular phylogeography addresses spatial patterns of evolutionary diversity within species or species complexes and has recently been expanded to include comparison of phylogeographic patterns of multiple co-distributed lineages, comparative phylogeography (Arbogast and Kenagy 2001). Such studies have revealed pervasive and unanticipated biogeographic patterns and suggest that biotic assemblages contain much greater cryptic biological diversity than traditional systematics has recognized (*e.g.*, Bird *et al.* 2007, Sha *et al.* 2007, Victoriano *et al.* 2008). In a comparative framework, phylogeography can be used to evaluate both historical patterns and evolutionary processes, providing a basis for new avenues of research into the regional historical, ecological, and coevolutionary factors generating and maintaining biodiversity.

The well-documented geological history and known ages of the Hawaiian Islands allow examination of the timing of lineage splitting and species formation. The phylogenetic pattern characteristic of Hawaii's more diverse endemic clades, especially nonvolant groups with limited active dispersal ability, is for the older, basal members of a clade to occur on the oldest island and for successively more recently derived members of the clade to occur on successively younger islands (Wagner and Funk 1995, Fleischer *et al.* 1998, Roderick and Gillespie 1998, Price and Clague 2002, Cowie and Holland 2006), a pattern termed the progression rule of island biogeography (Wagner and Funk 1995). Since land snails are generally considered poor active long-distance dispersers; they are predicted to adhere to the progression rule pattern on oceanic archipelagos.

Native invertebrates, among them the endemic land snails, comprise the most species-rich faunal radiations in the Hawaiian Islands and offer valuable opportunities for the study of historical biogeography and evolutionary diversification of insular radiations in a comparative phylogenetic framework.

HAWAIIAN LAND SNAILS AS BIOGEOGRAPHIC MODELS

Hawaiian land snail phylogenies provide opportunities to investigate a number of general issues in evolutionary biology, including the relative roles of dispersal versus vicariance in the generation and maintenance of endemic lineages and the predictions of the "taxon cycle" (*sensu* Wilson 1961).

Since the early 1980s, a debate has periodically flared up in the primary biogeographic literature regarding the importance of vicariance versus dispersal in shaping distributions of plants and animals. Since most species have patchy distributions at some scale, and patchiness or allopatry has long been considered to play an important role in diversification (Mayr 1942), the mechanisms contributing to natural distribution patterns are fundamental to evolutionary biology and our understanding of biodiversity (see de Queiroz 2005, Cowie and Holland 2006).

According to the predictions of Wilson's (1961) taxon cycle, island lineages initially colonize marginal habitat, eventually dispersing and diversifying into higher elevation cloud forests, and ultimately go extinct as habitat changes and islands erode and subside. One of the key features of Wilson's taxon cycle is the notion that oceanic islands serve as evolutionary blind alleys (Whittaker 1998) and, therefore, do not give rise to further long-distance colonization.

Also, the diverse Hawaiian land snails provide natural systems with which to use molecular techniques to investigate many such patterns of island biogeography and lineage splitting (Holland and Hadfield 2002, 2004, Rundell *et al.* 2004, Cowie and Holland 2006, Holland and Cowie 2007) as well as to address more basic systematics issues (Holland and Hadfield 2007).

HAWAIIAN SUCCINEIDAE

Succineids occur worldwide (Pilsbry 1948, Patterson 1971), reaching their highest diversity in Pacific islands, India, and the Americas (Barker 2001). Though often associated with riparian areas (*e.g.*, Kerney and Cameron 1979), succineids also occur in a range of different habitats (Barker 2001, Rundell *et al.* 2004). There are 42 recognized Hawaiian succineid species, all endemic, with 35 single-island endemics (Cowie *et al.* 1995), suggesting that dispersal between islands occurs, but is sufficiently rare to allow speciation. The Hawaiian Succineidae have radiated into a diverse array of habitats, from montane rainforests to xeric coastal dunes (Cowie 1995, Cowie *et al.* 1995). Their shell types appear to reflect these ecological differences, making them candidates for studies of adaptive radiation, convergence, and morphological evolution.

We have been unable to find approximately half of the described species despite intensive field efforts focused on type localities and other suitable habitat, *e.g.*, *Catinella rubida* Pease, 1870 from Kauai, the type species of the genus *Catinella* Pease, 1870. These species are either extremely rare or possibly extinct. Rundell *et al.* (2004) estimated that as many as one third of the Hawaiian succineid species may be extinct, but this may well be an underestimate.

Phylogenetics and biogeography

Although the family in the Hawaiian Islands was historically assumed to be monophyletic and the result of a single colonization (Zimmerman 1948), Rundell *et al.* (2004) showed, based on mtDNA evidence, that this is not the case. Here we present a global, multi-locus data set that permits this surprising biogeographic result to be investigated further.

A combined multi-locus phylogeny of 40 ingroup species indicates that the Hawaiian succineids fall into two monophyletic groups (Fig. 2). Clade A (Fig. 2) includes succineids from Kauai, Oahu, Molokai, Maui, Lanai, and Hawaii, with a species from Samoa nested within this clade, sister to a species from Kauai. The general patterns of relationships within this clade provide support, though weakly, for the progression rule of successive colonization from older islands (Kauai, 5.1 Ma, Oahu, 3.7 Ma) to younger islands (West Maui, 1.3 Ma, Hawaii, <0.5 Ma), with species from Kauai and Oahu associated with the basal nodes of the clade. Basal to this clade is a species from the islands of the South Pacific (Samoan, Marquesas, Cook, and Austral Islands), indicating an ancient South Pacific origin. Clade B includes species from the island of Hawaii plus *Succinea caduca* Mighels, 1845, which is the one Hawaiian succineid that occurs on all six main islands (Holland and Cowie 2007), with a species from Tahiti nested within the clade, sister to a species from the island of Hawaii. Basal to Clade B is a species from Thailand (that is also found as a modern invasive species in Hawaii), suggesting a southeast Asian origin. Clade A is the older of the Hawaiian succineid lineages. The endemic Hawaiian succineids are not monophyletic and the two main Hawaiian lineages differ in their geographic origin and inferred relative time of colonization.

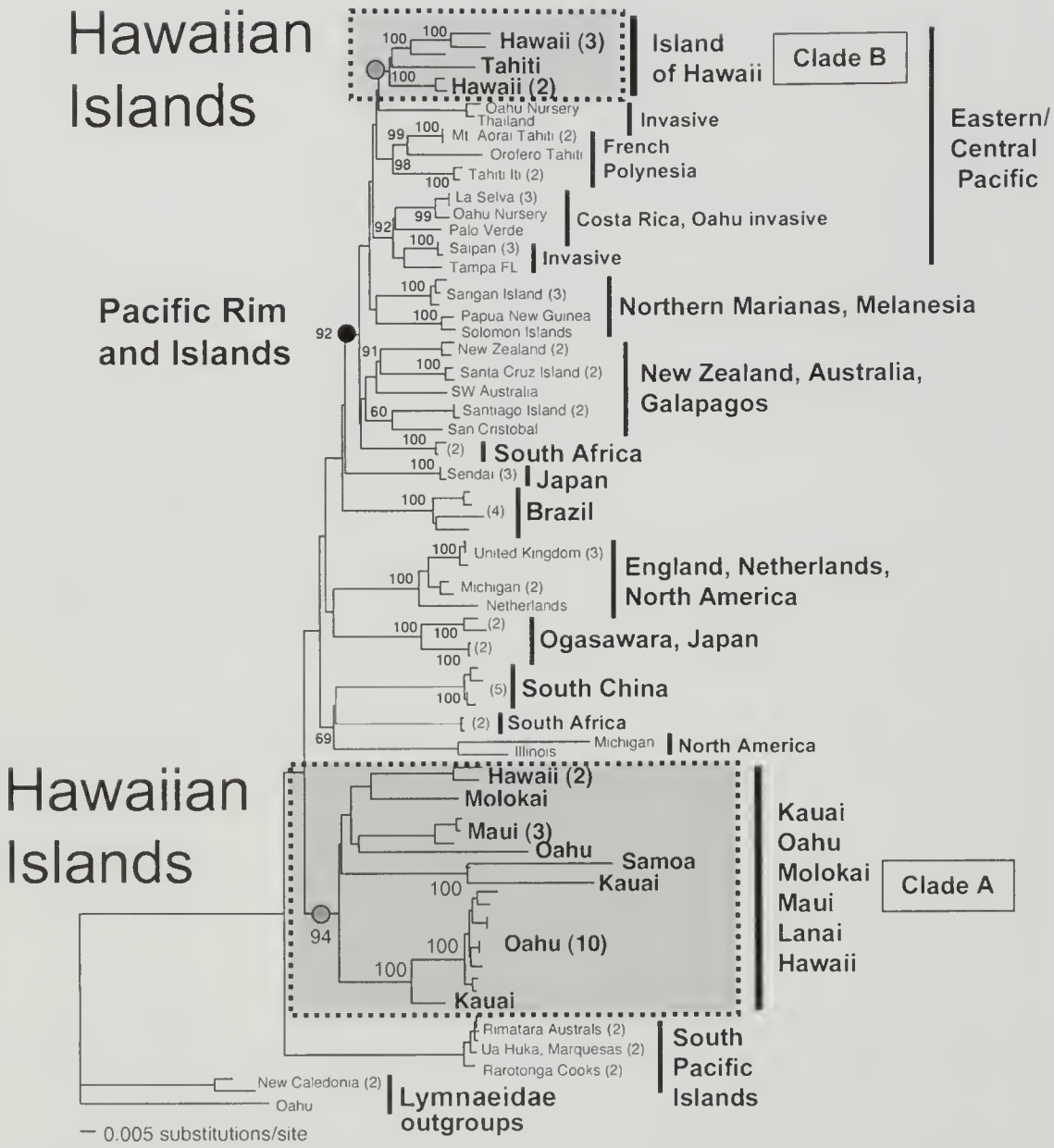

Figure 2. Phylogenetic tree for the Succineidae, based on three genes, two mitochondrial and one nuclear (COI, 16S, 18S; 1740 base pairs), for 40 ingroup species and two outgroups. This area phylogram was generated with PAUP (Swofford 2002) using a maximum-likelihood approach. Numbers near nodes represent bootstrap support based on 1000 replicates. Numbers in parentheses show numbers of specimens sequenced per lineage. The shaded boxes highlight the two Hawaiian lineages.

An Asian or Australasian origin has been thought likely for a number of other Pacific island land snail groups (Cowie 1996, Pokryszko 1997). The phylogenetic analyses presented here, with Thai species basal to Clade B (Fig. 2), are consistent with this suggestion. The positions of a Samoan species in Clade A and a Tahitian species in Clade B suggest that Samoa was colonized from Kauai and Tahiti was colonized from Hawaii. These may be the first recognized cases of natural colonizations of other locations by endemic Hawaiian animal species, contrasting, since they are both rainforest not marginal habitat species, with predictions of Wilson's (1961) "taxon cycle", which considers endemic island lineages to be essentially evolutionary blind alleys.

The absolute ages of the Hawaiian succineid lineages are uncertain but theoretically an ancestral succineid could have arrived in the Hawaiian archipelago as early as about 29 Ma ago. This is the age of Kure, the adjacent older islands in the chain having already vanished below the ocean surface, and islands have been consistently present above sea level since then (Carson and Clague 1995, Clague 1996). However, many groups of Hawaiian plants and animals exist exclusively at high elevation. Therefore, since there were probably periods of hundreds of thousands of years when, as older islands subsided and eroded and newer islands were as yet low, only low elevation habitats were available. Absence of high elevation habitat may thus preclude an ancient origin (*i.e.*, 29 Ma) (Price and Clague 2002). In particular, such a scenario may

have happened when Kauai, the oldest, high island, emerged because Nihoa (the adjacent older island) had already declined greatly in elevation (Price and Clague 2002). Nevertheless, some modern Hawaiian succineids inhabit coastal dune lands and low-elevation forests, indicating that their ancestors could also have thrived in similar environments; land of sufficient, if low, suitable elevation was indeed consistently available from 29 Ma ago to the present. Archaeological and paleontological evidence suggests that succineids, amastrids, and other endemic Hawaiian land snail species probably once had ranges that extended into low elevation dry forest and arid habitats (Christensen and Kirch 1986). Phylogenetic studies of other Hawaiian invertebrate radiations suggest a few origins far exceeding the age of Kauai (Russo *et al.* 1995, Jordan *et al.* 2003).

The island of Hawaii is less than 0.5 Ma old, and 22 (19 endemic) of the 42 recognized Hawaiian succineid species are from this island (Cowie *et al.* 1995). Additional work on the evolution of succineid species on the island of Hawaii, such as application of molecular clock theory to robust phylogenies consisting of additional nuclear genes and the possible inclusion of extinct species from museum collections, may provide more insights into the complexity and rate of evolutionary change.

Single species phylogeography: *Succinea caduca*

Although the Hawaiian succineids are primarily single-island endemics, *Succinea caduca* Mighels, 1845 occurs on all six major high islands (Holland and Cowie 2006). Holland and Cowie (2007) used mtDNA COI sequences to evaluate geographic patterns of variation in *S. caduca*, sampling 24 populations on the six islands. Six clades based on 276 COI sequences were revealed, indicating substantial geographic genetic structuring. Low nucleotide diversity and low pairwise molecular-divergence values within populations coupled with higher between-population values suggested multiple founder events. High overall haplotype diversity suggested diversification involving rare dispersal, fragmentation by historical lava flows, and variation in habitat structure. Within-island rather than between-island population comparisons accounted for the majority of molecular variance. Population partitioning patterns suggested that genetic fragmentation has been driven by punctuated, passive dispersal of groups of closely related haplotypes that subsequently expanded and persisted in isolation for long periods (average >2 Ma), and that inter-island dispersal has led to population fragmentation. However, Mantel tests for isolation by distance, statistical correlation of geographic and genetic distance, were not significant. Thus, rather than a widespread panmictic distribution that was subsequently divided into its present day distribution, we see evidence that dispersal has led to a chaotic pattern of genetic partitioning. Historical availability of mesic coastal habitat, together with effective dispersal, may explain the long-term persistence and unusual multi-island distribution of this species, which contrasts with the single island endemism of most Hawaiian succineids as well as much of the Hawaiian biota (Holland and Cowie 2007).

Haplotype networks from the northwestern portion of the archipelago, representing the older islands of Kauai and Oahu that are separated by the Kauai Channel (Fig. 1) and have never been connected, are broken into 5 clades (Holland and Cowie 2007). One of these clades contains haplotypes from Kauai and Oahu, demonstrating unambiguously that dispersal across the Kauai Channel has occurred. Other haplotypes from Oahu and all those from Maui Nui (Maui, Molokai, Lanai) group in a single clade and provide support for vicariant separations and evidence that Pleistocene island connections may have been important in enhancing gene flow. Vicariant separation in this clade has not led to deep divergence, a reflection of the geologically recent separation of the Maui Nui component islands (Price and Elliott-Fisk 2004), which conforms with the estimated most recent sea level minimum at the last glacial maximum 18,000 years ago, about 130 m below the current level. Haplotypes from the island of Hawaii cluster in a separate, single island clade. Thus, *Succinea caduca* provides evidence for both within (Kauai, Oahu) and between (Kauai–Oahu, Maui–Hawaii) island diversification, suggesting that a combination of vicariance and dispersal has led to the allopatric diversification of this species.

HAWAIIAN ACHATINELLINAE

With 99 recognized species, all single-island endemics, in four genera (Cowie *et al.* 1995, Holland and Hadfield 2004), the endemic Hawaiian tree snails (Achatinellinae) are a species-rich radiation. The richly colored, highly varied banding patterns of their shells captured the attention of early naturalists and shell collectors, many of whom collected thousands of snails during the late 1800s and early 1900s (Hadfield 1986). Historically, appreciation for Hawaiian tree snails helped to inspire and promote general awareness of the diverse and unique Hawaiian biota. In recent years, however, the Hawaiian tree snails have also gained scientific and regulatory attention because of their dire conservation status. Of the 41 species of *Achatinella* Swainson, 1828 recognized by the U.S. Fish and Wildlife Service, only 10 are now thought to survive and are listed as endangered, with range reductions approaching 90% (U.S. Fish and Wildlife Service 1993). All other achatinelline species are seriously threatened.

Phylogenetics and biogeography

The molecular phylogenetic pattern for the Hawaiian tree snails (Fig. 3; see also Thacker and Hadfield 2000, Holland and Hadfield 2004) contrasts markedly with the topology for Hawaiian succineids (Fig. 2). The extant species analyzed

form a monophyletic group of three main clades: the Oahu Clade (1) consisting only of five *Achatinella* species from Oahu; the Maui Nui Clade (2) with 13 species from three genera and four islands (Oahu, Molokai, Lanai, Maui); and the Mixed Clade (3) with five species from three genera and four islands (Oahu, Molokai, Maui, Hawaii). The outgroup (*Auriculella* sp., Achatinellidae: Auriculellinae) was selected based on Holland and Hadfield (2004).

Achatinella mustelina Mighels, 1845, endemic to the oldest mountain range on the island, was basal to the other four members of the clade. Therefore, in reconstructing the biogeographic pattern and colonization sequence for the tree snails (Fig. 4), we begin with *A. mustelina*. As few as two of the twelve colonization events depicted in Fig. 4 may have involved dispersal over an ocean channel; the remainder could have taken place via past island connections (forested land bridges) and relatively recent vicariant separation. However, this is the minimum possible number of ocean channel crossings based on this analysis.

The following genetic divergence values were generated using mtDNA COI sequence data, for which published divergence rates for invertebrates are typically in the range of 1.4 to 2.2% per million years (Knowlton and Weigt 1998). The mean divergence among the 12 species of *Partulina* Pfeiffer, 1854 (5.4%) was lower than that among the *Achatinella* species, all from a single island (6.1%), despite the *Partulina* species coming from what are presently four islands (Maui, Molokai, Lanai, Hawaii) (Fig. 1), suggesting that the *Partulina* and *Perdicella* species in the Maui Nui Clade are younger than *Achatinella* species. The mean genetic divergence among species of all three genera from the Maui Nui Clade was 5.4%, slightly lower than that for all members of the genus *Partulina* at 5.5%. Interestingly, the divergence between *Partulina physa* (Newcomb, 1854) from the island of Hawaii and the next closest relative, *P. tappaniana* (Adams, 1851), was low (3.3%) in spite of substantial differences in shell morphology and separation of the islands by the Alenuihaha Channel. This relatively close relationship, spanning a deep marine feature, reflects historical dispersal across a marine barrier.

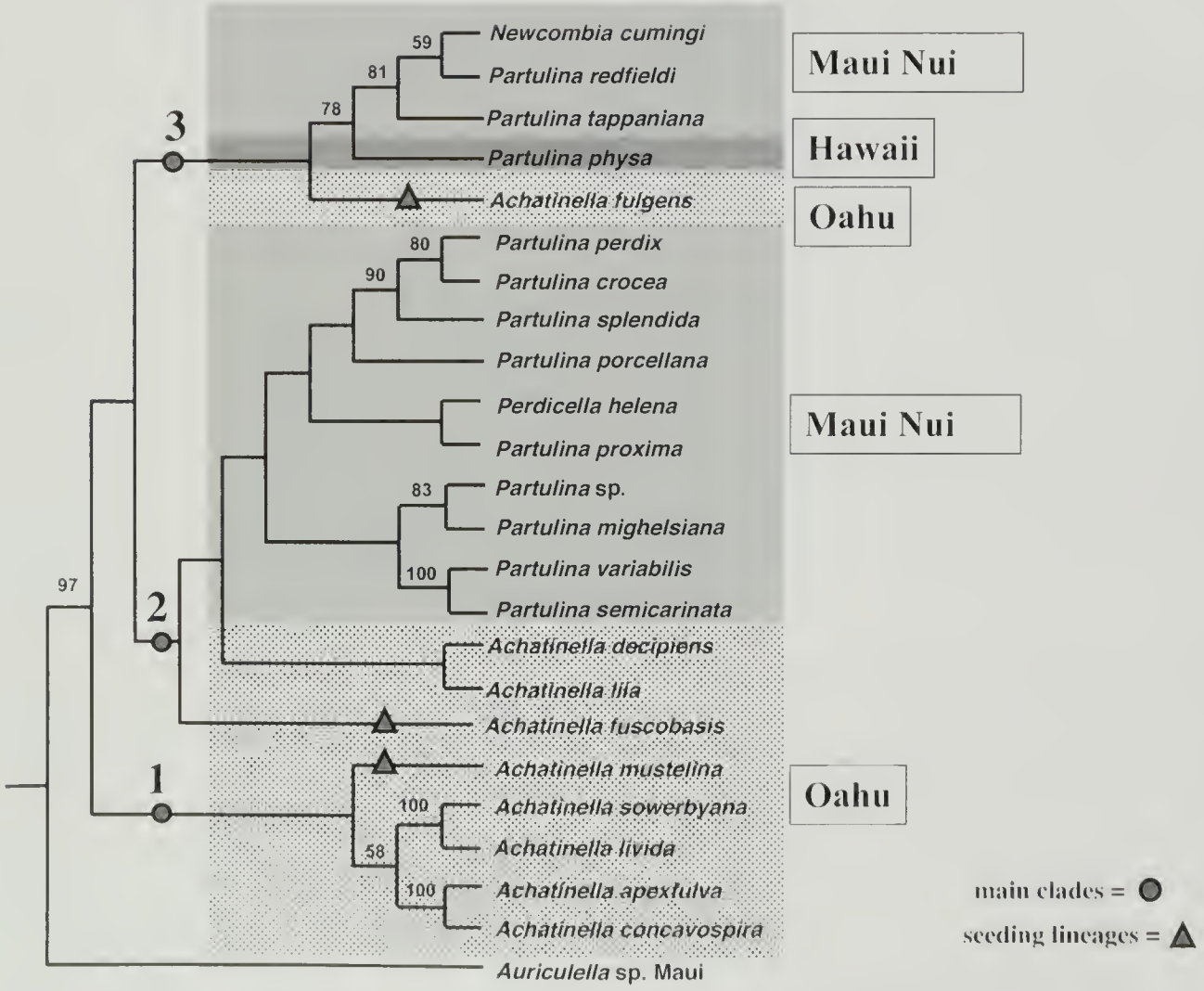

Figure 3. Maximum likelihood cladogram generated using PAUP (Swofford 2002) for the achatinelline tree snails reconstructed using COI gene sequences and 1000 bootstrap replicates. Some of the main features include monophyly of the subfamily and family (see Holland and Hadfield 2004), progression rule pattern of biogeography, and presence of seeding lineages from the oldest island in the group in each of the three main clades.

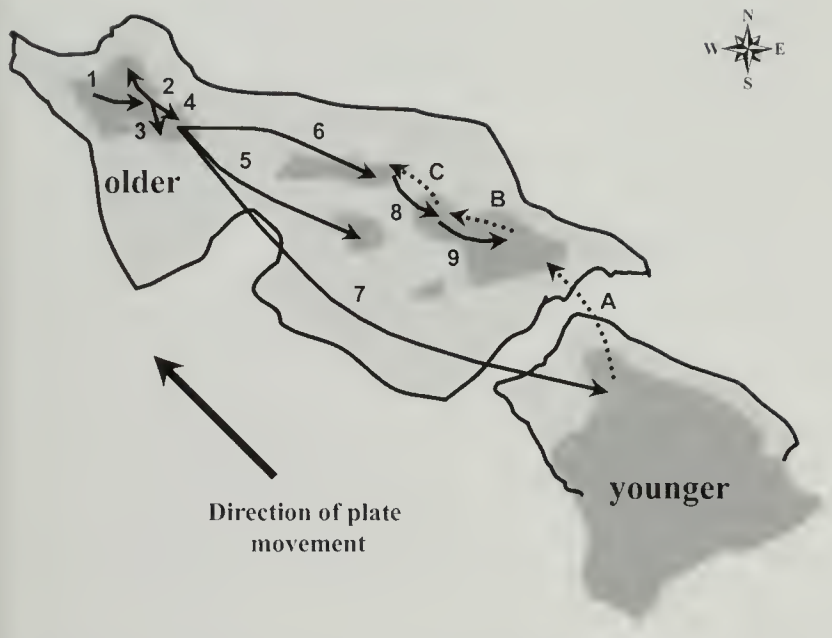

Figure 4. Island colonization sequence inferred from molecular evidence for achatinelline tree snails, based on the phylogeny of Holland and Hadfield (2004). Map includes submarine historical shorelines. Solid arrows follow the progression rule and represent forward colonization events from older to younger geological features, numbered according the order of the nodes in the tree (Fig. 3) and starting from *Achatinella mustelina*. Dotted arrows show back colonizations, from newer to older geological features or islands.

In a phylogenetic reconstruction that includes species representing all five achatinellid subfamilies, the Achatinellinae are monophyletic and well supported (R. H. Cowie *et al.*, unpubl. data). Achatinellid sequences formed a monophyletic group with high bootstrap support (91–100%).

Single species phylogeography: *Achatinella mustelina*

Holland and Hadfield (2002) used mitochondrial DNA (mtDNA) COI sequences to evaluate phylogeographic structure within and among 21 populations of *Achatinella mustelina* ($N = 78$). In contrast to the multi-island distribution of *Succinea caduca*, *A. mustelina* has a relatively small distribution spanning a single mountain range on Oahu. Pairwise intraspecific mtDNA sequence divergence between haplotypes ranged from 0 to 5.3%, and population genetic partitioning and mountain topography were strongly correlated. Maximum genetic distances were observed across deep, largely deforested valleys and sheer mountain ridges, independent of geographic distance. However, in certain areas where forest cover is presently fragmented, there was little sequence divergence despite large geographic distances. Genetic data were used to define five evolutionarily significant units (ESUs) that will guide conservation decisions regarding, for instance, placement of predator-exclusion fences, captive propagation, and eventual re-introduction and translocation.

To account for the observed phylogeographic pattern, an evolutionary scenario was proposed (Holland and Hadfield 2002) beginning with an initial panmictic phase, followed by long-term, large-scale habitat fragmentation, and finally recent fine-scale fragmentation resulting in the current patchy distribution. In the early geological history of the island, western Oahu consisted of a single massive shield volcano, similar in shape to the less than half-million year old volcanoes on the island of Hawaii. The modern topography of western Oahu is deeply eroded and rugged, with complex features resulting from action of wind and rain over its 3.7 Ma history. It is possible that large populations of tree snails gradually became separated from one another by vicariant forces resulting from the formation of valleys and ridges, and isolated by distance into the present pattern of "islands" of genetically cohesive populations. In support of this idea, a Mantel test (Holland and Hadfield 2002) demonstrated a correlation between genetic and geographic distance (in contrast to *Succinea caduca*). *Achatinella mustelina* has a far more restricted and genetically structured distribution than *S. caduca*, indicating relatively limited dispersal ability, possibly related to the former's much larger and heavier shell.

CONCLUSIONS

The molecular studies of Hawaiian land snails reviewed here strongly support the current shift in perception in historical biogeography from vicariance as the dominant process to more of a balance between dispersal and vicariance driving allopatric diversification.

In the Hawaiian Succineidae, molecular data reveal two independent colonization events from two different, distant geographic origins. Once the two lineages became established and began to radiate, each acted as a colonization source for long-distance dispersal to two different South Pacific island groups. Within one Hawaiian succineid lineage, dispersal across marine barriers occurred multiple times, resulting in one species (*Succinea caduca*) that occurs on all six major high islands. Closely related haplotypes that span a deep permanent feature such as the Kauai Channel attest to the dispersal ability of this species.

For the Hawaiian tree snails dispersal has also helped to shape their natural history in important ways. Sister species that span the Alenuihaha Channel between the relatively young islands of Maui and Hawaii attest to recent across-ocean dispersal. However, the fact that all 99 species are single-island endemics indicates that dispersal of these sedentary, heavy-shelled tree snails, while it certainly has occurred, is rare. Patterns of molecular diversification in the achatinellines indicate an Oahu origin, progression rule pattern, isolation by distance, and at least two channel-crossing dispersal events.

In contrast to the deep separation of two distinct lineages in the succineids, the achatinellines form a monophyletic clade (Holland and Hadfield 2004). However, preliminary molecular data indicate that the family Achatinellidae, which consists of five subfamilies (Cowie *et al.* 1995), two of which are endemic to Hawaii, colonized the Hawaiian Islands via four independent events (Holland and Cowie, unpubl. data).

Based on the well understood geological history of the Hawaiian Islands and the use of molecular phylogenetics, it has been possible to reconstruct the evolutionary and biogeographical history of two major groups of land snails, including the timing of lineage splitting and direction of colonization, while at the same time determining their geographic origins and whether presumptive radiations comprise monophyletic groups. Because of the relatively sedentary nature of land snails, yet the proclivity of some for long-distance passive dispersal, these groups have facilitated a major insight into the mechanisms via which evolutionary diversification takes place. Important phylogenetic lessons emerging from these studies of island snails include: (1) assumptions of monophyly are not always met; (2) in multi-island lineages composed of single island endemic species, monophyletic clades may include species from different islands; and (3) although some lineages conform to the isolation by distance and progression rule patterns of biogeography, others do not. Studies of island land snails will eventually lead to estimations of ages of species groups, speciation rates, timing of the processes involved in community assembly, and other dynamics, all of which are important contributions to the overall understanding of mechanisms of evolution.

ACKNOWLEDGMENTS

We thank Matthias Glaubrecht and Thomas von Rintelen for inviting us to participate in the symposium they organized and for the invitation to write this contribution. Our work on Succineidae was supported by NSF grant DEB 0316308. Molecular phylogeographic analysis of Hawaiian tree snails was carried out in the laboratory of Michael G. Hadfield, to whom we are grateful.

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Submitted: 9 November 2008; **accepted:** 23 January 2009;
final revisions received: 16 March 2009